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COMPARATIVE GAS EXCHANGE OF LEAVES AND BARK IN THREE STEM SUCCULENTS OF BAJA CALIFORNIA¹

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Arborescent stem succulents in tropical and subtropical deserts depend on scarce and uncertain rainfall. Gas exchange and the diurnal acidity fluctuation of bark and ephemeral leaves were measured under both dry and moist soil conditions in *Fouquieria columnaris* (cirio or boojum tree) and *Pachycormus discolor* (torote blanco or elephant tree) and in stems of the columnar cactus *Pachycereus pringlei* (cardon) in the Central Desert of Baja California, Mexico. Results demonstrated that ephemeral leaves were the only site of exogenous CO₂ assimilation in *F. columnaris* and *P. discolor*; there was no measurable gas exchange across the green photosynthetic bark. The pattern of gas exchange in *F. columnaris* and *P. discolor* was consistent with that of C₃ plants. *P. pringlei* was shown to be a typical Crassulacean acid metabolism plant on the basis of acid fluctuations and gas exchange. Chlorophyll fluorescence studies of the green bark of *F. columnaris* and *P. discolor* indicated that this tissue is photosynthetically functional, and that CO₂ assimilation can rise above the compensation point under high CO₂ concentrations, such as may occur within the plant. The green photosynthetic bark of these species may be an adaptation for surviving prolonged drought and may function to recycle endogenous respiratory CO₂, thus maintaining the plant's energy reserves and permitting rapid production of leaves in response to infrequent rains.

The vegetation of warm deserts frequently contains a high proportion of arborescent species with photosynthetic stems. One important group is the succulents with Crassulacean acid metabolism (CAM) (Kluge and Ting, 1978; Winter, 1979). Another group comprises C₃ woody plants that have stomata or other structures in the bark surface that permit gas exchange (Adams and Strain, 1969; Schaedle, 1975; Szarek and Woodhouse, 1978). A third group is composed of plants that have

stems with translucent exfoliating bark, a large amount of parenchymatous tissue that serves as a water reservoir, and non-succulent ephemeral leaves (Henrickson, 1972; Gibson, 1981; Ihlenfeldt, 1985). Bark photosynthesis in these non-CAM stem succulents has not been adequately investigated.

Bark photosynthesis helps to maintain adequate carbohydrate supplies during the leafless period and also serves to refix (recycle) respiratory CO₂. It is an important adaptation that permits reassimilation of the bulk of respiratory CO₂ evolved by stems of some desert plants (DePuit and Caldwell, 1975).

The distinctive perennial vegetation of the Central Desert of Baja California, Mexico, owes its bizarre appearance largely to the presence of such arborescent stem succulents as boojum tree (*Fouquieria columnaris*) and elephant tree (*Pachycormus discolor*). These plants can survive 5 or more years without rain (Nelson, 1921) and are well suited for studying the adaptation of plants to prolonged drought and uncertain rain.

Ocotillo (*Fouquieria splendens*) Engelm., which is a closely-related species to *Fouquieria columnaris*, has non-succulent green stems that do not fix exogenous CO₂ but do reassimilate

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endogenous CO₂ and maintain adequate carbohydrate supplies during periods of prolonged drought, resulting in rapid refoliation in response to rainfall events (Mooney and Strain, 1964). Nedoff, Ting, and Lord (1985) suggested that uptake of exogenous CO₂ does not occur in *F. splendens* because the chlorenchymatous tissue occurs beneath impermeable cork, and no evidence was found for lenticels or other structures that would permit gas exchange across the cork.

The objectives of this study were to determine: 1) the photosynthetic pathways of leaves and stems in two species of stem succulents with translucent exfoliating bark, boojum tree (cirio) *Fouquieria columnaris* (Kellogg) Henrikson (Fouquieriaceae) and elephant tree (torote blanco) *Pachycormus discolor* (Benth.) Coville (Anacardiaceae); 2) whether exogenous CO₂ is assimilated by stem chlorophyll; and 3) whether water stored in succulent stem tissues is protected from external evaporative demand by the translucent bark. The photosynthetic patterns of the two microphyllous stem succulents were compared with those of the columnar cactus, cardon (*Pachycereus pringlei*) (S. Wats.) Britt. & Rose (Cactaceae).

MATERIALS AND METHODS

Study site—The study site was 1 km NE of Cataviña, Baja California, Mexico (29°44'N, 114°42'W). The location is an old erosion surface (550 m altitude) that consists of a granite bedrock interspersed with large boulders. The bedrock is overlain by a moderately deep (50–100 cm), structureless coarse sandy soil of decomposed granite. Annual precipitation averages 110 mm with approximately 80% falling during winter frontal storms and only 20% during summer convective storms (years of record 1957–1987; unpublished data of the Secretaría de Agricultura y Recursos Hidráulicos, División Hidrométrica, Ensenada, Baja California). Daytime temperatures frequently exceed 40 °C during summer, but there are only a few freezing nights during winter. The perennial vegetation consists of two strata: the shrub stratum (<2 m height) is dominated by *Larrea tridentata* (Sessé & Moc. ex DC.) Coville, and includes *Eriogonum fasciculatum* Benth., *Ambrosia chenopodifolia* (Benth.) Payne, *Simmondsia chinensis* (Link.) Schneider, *Ferocactus gracilis* Gates, *Opuntia molesta* Brandegee, and *O. cholla* Weber; the arborescent stratum (>2 m height) includes *Pachycormus discolor*, *Pachycereus pringlei*, *Fouquieria columnaris*, *F. splendens*, *Prosopis glandulosa* Torr., and *Bursera microphylla* A. Gray.

Soil water potentials—Soil water contents at 0–10, 10–30, 30–50, and 50–100 cm were determined gravimetrically (Gardner, 1986) from soil samples obtained from clear areas between shrubs using an 8-cm-diameter soil auger at three locations within the sampling site. Soil water potential was estimated from moisture characteristic curves obtained from one soil core using a thermocouple psychrometer (NT-3 nanovoltmeter thermometer, Decagon Devices, Pullman, WA) (Klute, 1986; Rawlins and Campbell, 1986).

Leaf water potentials and titratable acidity—Leaf water potentials were measured on secondary shoots or “side branches” of *F. columnaris* and on twigs of *P. discolor* using a pressure chamber (PMS Model 1000, PMS Instrument Co., Corvallis, OR). The green tissue was separated manually for titration from four stem samples taken with a #5 cork borer (1 cm diameter). Leaf samples of *F. columnaris* consisted of four secondary-shoot leaves and of entire leaflets of *P. discolor*. Separate leaf samples were collected on both sampling dates, and leaf areas were measured in order to present the titration data on an areal basis. Samples were ground in distilled water and titrated to a pH 7.0 endpoint with 0.01 N KOH.

Gas exchange and fluorescence kinetics—A fully portable system (consisting of a leaf chamber, air supply, and infrared gas analyzer units) operating in the open mode was used to measure leaf gas exchange in the field (LCA-2 System, The Analytical Development Co. Ltd., Hoddesdon, Herts, England). The leaf chamber, within which a portion of the leaf was sealed during measurements for about 30 sec, contained a solid-state humidity sensor, a thermistor for air temperature measurements, and a quantum sensor for photosynthetically active radiation (PAR) measurements. For gas exchange measurements of the bark surface, the instrument's leaf chamber was replaced by an open cuvette (4 × 7 × 1 cm) constructed of clear Plexiglas of 2.5 mm thickness. An airtight gasket (1 cm thick) of adhesive foam rubber with closed pores was attached to the basal side of the cuvette to make a firm tight seal with the stem. The cuvette was pressed against the stem and held in position during measurements. Air was circulated with a miniature Micronnel fan (Type 249k-6V) to remove the boundary layer.

Gas exchange rates were determined from flow rates, projected leaf or stem surface area sealed within the chamber, and CO₂ and water vapor concentration differences between ref-

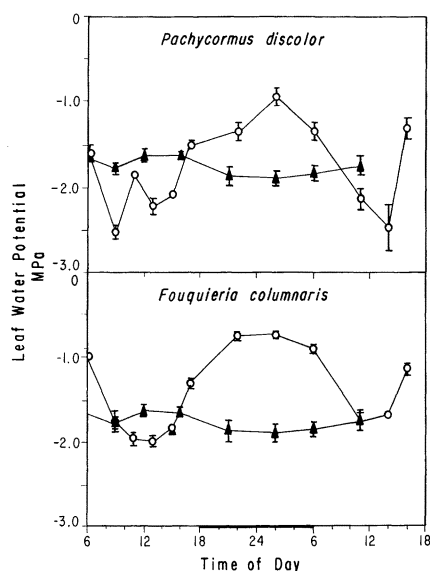


Fig. 1. Daily courses of leaf water potentials in *Pachycormus discolor* and *Fouquieria columnaris* during dry (3–4 December 1987; closed symbols) and moist (28–29 January 1988; open symbols) soil conditions. Horizontal bar below the x axis indicates the dark period. Vertical bars are ± 1 standard error of the mean ($N = 3$).

erence and analysis air. Gas exchange was calculated according to von Caemmerer and Farquhar (1981).

For simultaneous measurement of chlorophyll fluorescence and CO_2 evolution, branches of each species were cut in the late afternoon and the cut end immediately recut under water. The leaves were allowed to fully saturate overnight under a polyethylene cover. Large sections of bark from the main stem were cut in the field, immediately placed in plastic bags lined with moistened filter paper, sealed, and kept in an ice chest (without ice) until transferred to the laboratory 15 hr after excision.

Fluorescence induction was measured at room temperature using a fluorescence detector probe (Hansatech, Kings Lyn, Norfolk, U.K.) as described by Delieu and Walker (1983). Continuous fluorescence signals were produced by illuminating dark-adapted leaf or stem samples with blue actinic light (photon flux density $1,200 \mu\text{mol m}^{-2}\text{s}^{-1}$) provided by an air-cooled tungsten-halogen light source and reflected from a cold mirror.

The sample chamber used for fluorescence measurements was fitted with two taps that communicate with the external atmosphere. For CO_2 evolution measurements, gas of known CO_2 concentration was fed from the inlet at 150 ml min^{-1} , and the CO_2 concentration of the outgoing air stream was monitored in the absolute mode with an ADC LCA-2 portable

TABLE 1. Mass-basis soil water contents ($\theta_{\text{dry weight}}$) and estimated soil water tensions ($\psi_{\text{soil water}}$) of the soil profile at Cataviña, Baja California, Mexico, during dry (3–4 December 1987) and moist soil conditions (28–29 January 1988)

Soil depth (cm)	Dry		Moist	
	θ_{dw}^a (%)	ψ_{dw}^b (MPa)	θ_{dw}^a (%)	ψ_{dw}^b (MPa)
0–10	0.41 (0.19)	–18.9 ^c	4.91 (0.31)	–0.35
10–30	1.51 (0.14)	–2.1	5.56 (0.33)	–0.24
30–50	1.14 (0.15)	–3.4	5.86 (0.40)	–0.22
50–100	1.08 (0.02)	–3.8	4.27 (0.24)	–0.37

^a Mean (standard error of the mean) ($N = 3$).

^b Calculated from water characteristic curves determined by thermocouple psychrometry from samples of whole air-dry soil taken from a single core ($N = 6$ for each curve).

^c Extrapolated value; soil water content was outside the range of water contents used to determine the water characteristic curve.

infrared gas analyzer (IRGA). Water vapor in the air stream was removed by passing through a column of magnesium perchlorate before entering the IRGA. Net assimilation was calculated as in von Caemmerer and Farquhar (1981).

RESULTS

Soil and plant water status—Soil water content, leaf water potential, and gas exchange were first measured during 3–4 December 1987 after the summer drought had been broken by small precipitation events in October and November. *F. columnaris* and *P. discolor* had fully developed leaves at that time, but most of the available water had been removed from the soil profile (Table 1) during 4 weeks of dry weather. At that time the diurnal cycle of leaf water potential for both species did not exhibit large fluctuations (Fig. 1), indicating that neither species was actively transpiring. Thereafter, strong frontal storms (17–18 December 1987, 53 mm; 17–19 January 1988, 53 mm) recharged the soil profile. Soil water was available and the vapor pressure deficit was much smaller (data not shown) when a new set of measurements were obtained on 28–29 January 1988 (Table 1; Fig. 1). At that time both *F. columnaris* and *P. discolor* showed strong diurnal fluctuations in leaf water potential, indicating that they were actively transpiring.

Titrateable acidity—The fluctuation of titrateable acidity in stems and leaves of *F. columnaris* and *P. discolor* during the two sampling dates and afterwards showed no consistent pattern and contrasts markedly with that of *P.*

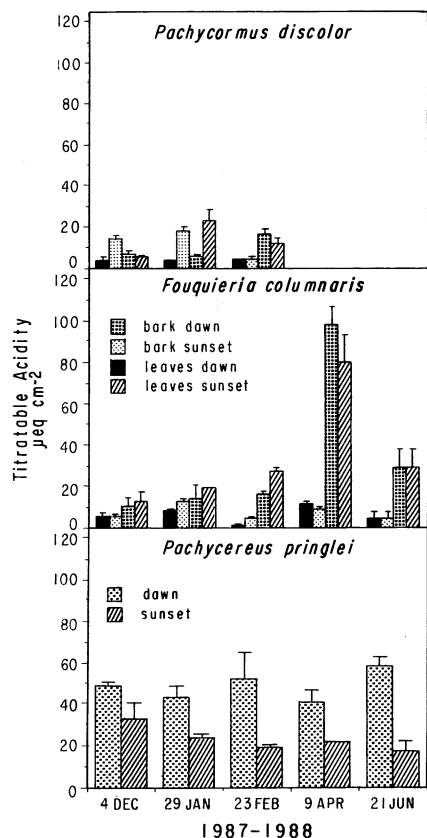


Fig. 2. Fluctuation of titratable acidity in leaves and bark of *Pachycormus discolor* and *Fouquieria columnaris*, and in bark of *Pachycereus pringlei* at dawn and sunset. Vertical bars are ± 1 standard error of the mean ($N = 4$).

pringlei, which presented a pattern consistent with CAM typical of cacti (Fig. 2). The leaves of both *F. columnaris* and *P. discolor* were yellowing and abscising on 9 April 1988; however, green *F. columnaris* leaves ground and titrated on that date contained anomalously high acidity, possibly connected with the senescence and abscission process. A few green leaves remained on *F. columnaris* as late as 21 June, but green leaves of *P. discolor* were unavailable in April and June.

Gas exchange and fluorescence kinetics—

Field sampling occurred during dry (3–4 December 1987) and moist (28–29 January 1988) soil conditions, and soil water potentials were accordingly different (Table 1). During both sampling periods the weather was sunny and warm the first day but increasingly cloudy and cool the second day (Figs. 3–5). The green photosynthetic bark of *Pachycereus pringlei* assimilated CO_2 and transpired during the nighttime, a pattern characteristic of CAM plants (Fig. 3).

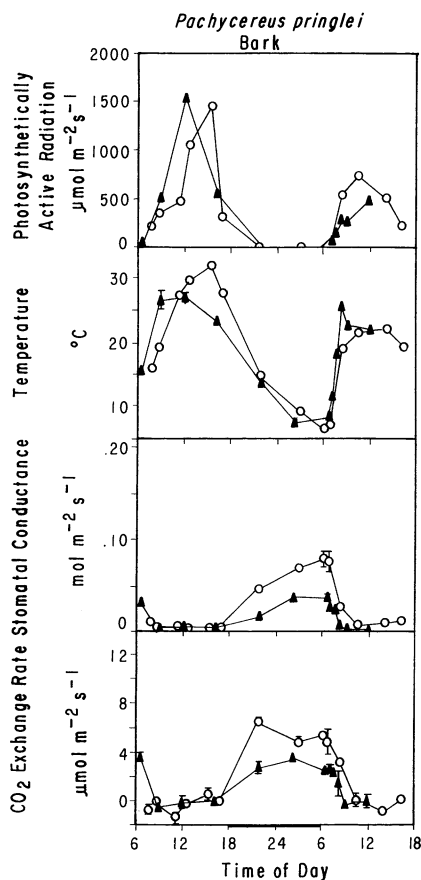


Fig. 3. Daily courses of photosynthetically active radiation, temperature, stomatal conductance, and CO_2 exchange rate for the bark surface of *Pachycereus pringlei* during dry (3–4 December 1987; closed symbols) and moist (28–29 January 1988; open symbols) soil conditions. Horizontal bar below the x axis indicates the dark period. Vertical bars are ± 1 standard error of the mean ($N = 3$).

Gas exchange was more active under wet than dry conditions.

Leaves of *F. columnaris* and *P. discolor* under water stress exhibited very low stomatal conductance and low CO_2 assimilation, but recharge of the soil profile after rains was accompanied by higher rates of transpiration and CO_2 uptake (Figs. 4–5). The green bark of *F. columnaris* and *P. discolor* did not show significant water vapor or CO_2 exchange during the course of the day under dry or moist soil conditions.

Figures 6 and 7 show chlorophyll fluorescence kinetics and CO_2 evolution of dark-acclimated leaf and stem samples after illumination. Upon illumination, fluorescence rose to a maximum very rapidly and gradually declined to a steady-state value after 2 min. This result indicates that the chloroplasts of both leaf and stem surfaces have the potential to

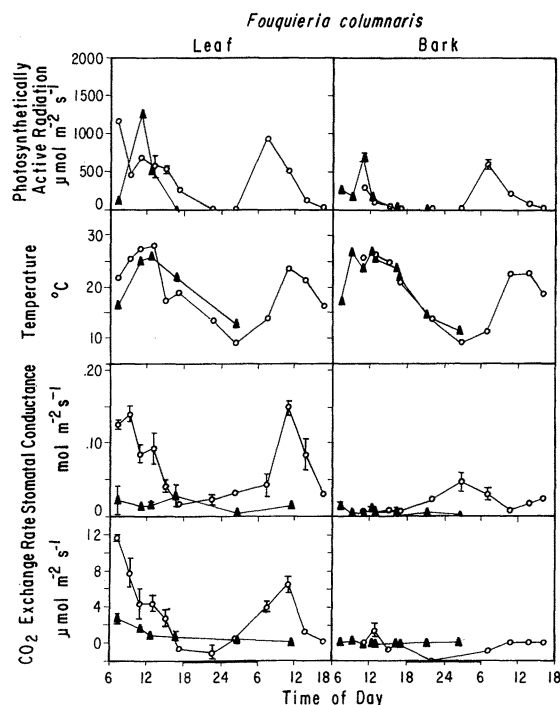


Fig. 4. Daily courses of photosynthetically active radiation, temperature, stomatal conductance, and CO_2 exchange rate for the leaf and bark surfaces of *Fouquieria columnaris* during dry (3–4 December 1987; closed symbols) and moist (28–29 January 1988; open symbols) soil conditions. Horizontal bar below the x axis indicates the dark period. Vertical bars are ± 1 standard error of the mean ($N = 3$).

photosynthesize. Although there were no significant differences in the fluorescence kinetics of the leaves and stem chloroplasts, CO_2 uptake exhibited different maximum asymptotic values after illumination. The initial dark respiration rates were different because the amount of bark tissue used during the experiment or the specific weight of the leaf samples were different. Carbon dioxide uptake in leaf and stem samples increased within seconds after illumination; however, the rate of increase of leaf CO_2 uptake was much higher than that of stem samples. In less than 2 min leaf photosynthesis was above the compensation point, and in about 3 min the leaf samples attained maximum asymptotic values in the range of $7\text{--}9 \mu\text{mol m}^{-2}\text{s}^{-1}$; whereas in stem pieces gross photosynthesis was only high enough to compensate for respiratory losses after a 3-min period.

The stem chlorophyll fluorescence not only responded to step increases in light levels but also to changes in ambient CO_2 concentrations. Figure 8 shows fluorescence kinetics and changes in net assimilation upon illumination

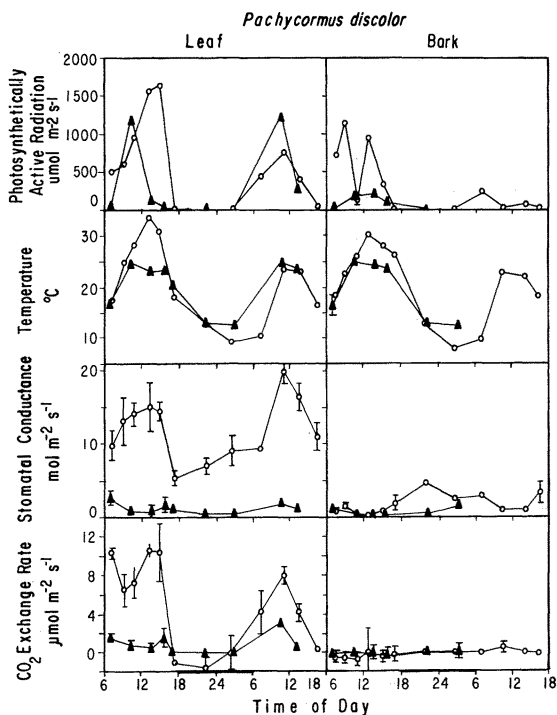


Fig. 5. Daily courses of photosynthetically active radiation, temperature, stomatal conductance, and CO_2 exchange rate for the leaf and bark surfaces of *Pachycormus discolor* during dry (3–4 December 1987; closed symbols) and moist (28–29 January 1988; open symbols) soil conditions. Horizontal bar below the x axis indicates the dark period. Vertical bars are ± 1 standard error of the mean ($N = 3$).

of stem samples of *F. columnaris* under two levels of external CO_2 concentration. Although the maximum initial fluorescence rise was similar, the asymptotic value was lower at high ambient CO_2 . The maximum net assimilation rate was higher under high CO_2 levels, as expected from chloroplasts that are functional and have the potential to assimilate carbon under adequate conditions.

DISCUSSION

Soil and plant water status—The diurnal cycles of leaf water potential and gas exchange for *P. discolor* and *F. columnaris* under wet and dry soil conditions demonstrate that stomata of both species are sensitive to changes in soil water potential (Table 1; Fig. 1). When soil moisture was abundant, soil water potential was approximately -0.3 MPa, and maximum overnight leaf water potential was about -1 MPa in both *F. columnaris* and *P. discolor*. However, during active daytime transpiration, leaf water potential reached a minimum of -2.0

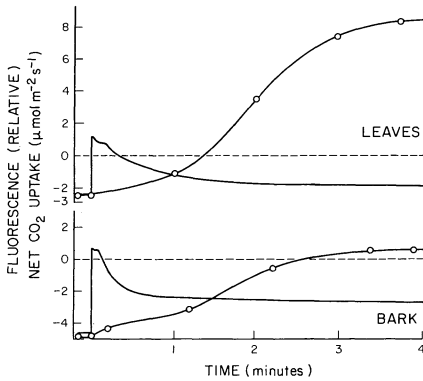


Fig. 6. Induction curves of fluorescence emission for leaves and bark of *Fouquieria columnaris* on exposure to actinic light (arrow) having a quantum flux density of $1,200 \mu\text{mol m}^{-2}\text{s}^{-1}$. The net CO_2 uptake of leaves and bark (open symbols) is shown throughout the experiments. The plant material was exposed to ambient CO_2 concentration during the measurements.

MPa in *F. columnaris* and -2.5 MPa in *P. discolor*, and leaves of *P. discolor* transpired more actively than those of *F. columnaris* (Figs. 4, 5). These results suggest that *P. discolor* may absorb more soil water than *F. columnaris* and water may be more available to it at lower soil water potentials.

Leaves of *F. columnaris* and *P. discolor* persist between rainy-season rainfall events. Short-term drought results in closed stomata and decreased carbon assimilation and water vapor loss. Long-term drought (as during the arid foresummer) results in leaf senescence and abscission. Water stored in the stems likely maintains an adequate plant water balance while soil moisture is unavailable.

Photosynthesis—The diurnal cycle of transpiration and CO_2 uptake in old stems of *P. pringlei* was typical of CAM plants. The four daily phases of CAM as defined by Osmond (1978) were more clearly apparent when water was abundant than under drought (Fig. 3). During phase III (when malic acid is decarboxylated and high CO_2 concentrations build up behind closed stomata), CO_2 efflux occurred under moist conditions but was much reduced under drought conditions. This result suggests that carbon was recycled more stringently during drought. The difference in titratable acidity in *P. pringlei* stems between sunrise and sunset increased from December to June; this implies an increased CAM activity by the cactus with increasing drought (Fig. 2).

Carbon dioxide absorption occurred in ephemeral leaves but not in old green stems of *F. columnaris* and *P. discolor* (Figs. 4–5). The pattern of gas exchange in the leaves of these

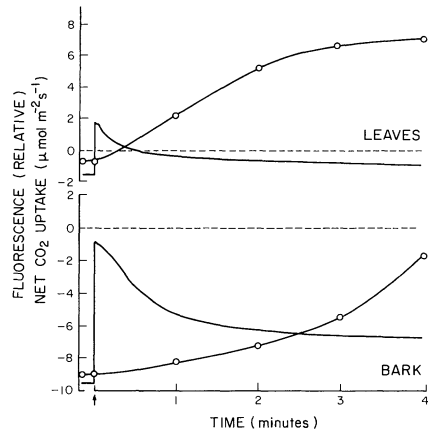


Fig. 7. Induction curves of fluorescence emission for leaves and bark of *Pachycormus discolor* on exposure to actinic light (arrow) having a quantum flux density of $1,200 \mu\text{mol m}^{-2}\text{s}^{-1}$. The net CO_2 uptake of leaves and bark (open symbols) is shown throughout the experiments. The plant material was exposed to ambient CO_2 concentration during the measurements.

species is consistent with that of C_3 plants. In both these species an encircling translucent periderm covers the chlorenchymatous tissue (Gibson, 1981; Henrickson, 1972) and presumably prevents gaseous diffusion. However, the trunks of *F. columnaris* have been observed to collapse and bend downward during prolonged drought (Henrickson, 1972), indicating that very slow water loss occurs over extended time periods. Nevertheless, the results obtained during dry soil conditions demonstrated that water stored in succulent stem tissues of both *F. columnaris* and *P. discolor* is protected from external evaporative demand by the bark.

The results reported here are similar to those obtained by Mooney and Strain (1964) and Nedoff, Ting, and Lord (1985) for *F. splendens*, a non-succulent Sonoran Desert xeromorph that is closely related to, but can survive more

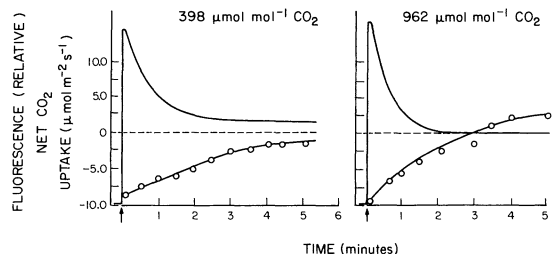


Fig. 8. Induction curves of fluorescence emission from *Fouquieria columnaris* bark on exposure to actinic light (arrow) having a quantum flux density of $1,200 \mu\text{mol m}^{-2}\text{s}^{-1}$. Before and during measurements, CO_2 concentrations were $398 \mu\text{mol mol}^{-1}$ or $962 \mu\text{mol mol}^{-1}$. The net CO_2 uptake (open symbols) is shown throughout the experiments.

extreme conditions than, *F. columnaris*. Nedoff, Ting, and Lord (1985) reported that stem chloroplasts of *F. splendens* were capable of assimilating CO₂ and indicated that exogenous CO₂ fixation does not occur "probably due to suberization of both types of cork cells and the absence of structures such as lenticels to allow CO₂ to reach the chloroplasts." Thus, the photosynthetic bark appears to serve the same purpose in both *F. columnaris* and *F. splendens*.

Photosynthesis by green stems and bark tissues is not uncommon among xerophytes (Adams and Strain, 1969; DePuit and Caldwell, 1975) and occurs as CAM in many arid zone succulents such as cacti and in some South African (Kluge and Ting, 1978) and Madagascar (Winter, 1979) species. Our results are consistent with these previous observations in that stem photosynthesis in *Pachycereus* is CAM, whereas the microphyllous stem succulents *Pachycormus discolor* and *Fouquieria columnaris* have C₃ metabolism.

Preliminary results indicated that about 50% of the incident light is transmitted across the translucent bark in *Pachycormus discolor* and *Fouquieria columnaris* (unpublished data). This indicates that sufficient light reaches the stem chloroplasts to activate the photosynthetic processes and may allow relatively high rates of carbon assimilation if the internal CO₂ concentration is not limiting. The fluorescence induction kinetics of dark-adapted stem sections indicated that the chloroplasts are photochemically competent, and there were no significant differences in the fluorescence kinetics of leaf and stem chloroplasts. Stem photosynthetic rates may be high enough to compensate for respiratory losses and may function to recycle endogenous respiratory CO₂ maintaining the plant's energy reserves and permitting rapid production of leaves in response to infrequent rains.

Thus, *Pachycormus discolor* and *Fouquieria columnaris* seem to exhibit convergent evolution of succulent water-storing stems that recycle endogenous CO₂ to ensure survival during extreme conditions, and non-succulent ephemeral leaves that permit high productivity during favorable environmental conditions.

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